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Decomposition of Angiosperm Tree Leaf Litter

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I. Introduction

The decomposition of tree leaves is not a problem which is entirely confined to the litter layer on the forest floor. In fact, processes of decay start from the very moment the leaf is formed, and the leaves are exposed to attack by micro-organisms and animals during their whole life, senescence and death. In this chapter, therefore, there will be emphasis on the description of the whole series of events related to breakdown or loss of material, from the moment of unfolding of the leaves until the final disappearance of the fallen litter and incorporation of its remnants into the organic fraction of the underlying soil.

II. Decomposition Processes in the Tree Canopy and Leaching of Nutrients by Precipitation

A. Nature and Activity of the Phylloplane Microflora

The phylloplane as a habitat for saprophytic or weakly parasitic micro-organisms has been a rather neglected field of study, as was pointed out by Ruinen (1961), but since then a considerable amount of literature has been published (Last and Deighton, 1965; Leben, 1965; Mangenot, 1966*a*; Preece and Dickinson, 1971; Pugh, Chapter 10).

It has been shown that tree leaves are invaded by micro-organisms very rapidly after unfolding. Holm and Jensen (1972) found several million bacteria per g dry weight of *Fagus* leaves which had been unfolded for only 1–2 days. Yeasts and filamentous fungi can also be demonstrated on recently unfolded leaves. The source of infection represents no problem in evergreen forests, where micro-organisms can easily transfer from old to new leaves. This is not possible in the deciduous forest following the long dormant period, but it has been demonstrated that buds may serve as a site for season-to-season carry-over of bacteria and fungi (Leben, 1971, 1972). Bacteria, yeasts and filamentous fungi have all been found in dormant buds of many different deciduous tree species (Keener, 1950, 1951; Davenport, 1966; Hislop and Cox, 1969; Pugh and Buckley, 1971*a*).

The phylloplane microflora in deciduous stands consists of relatively few species, especially at the beginning of the growing season. This indicates a rather extreme environment, probably due to the exposure to changing weather conditions, the limited availability of nutrients, and possibly the presence of antimicrobial substances (Topps and Wain, 1957; Beck *et al.*, 1969). Usually, the selectivity of the phylloplane environment diminishes during the growing season. It is also much less pronounced in the humid tropics than in cool temperate regions. The phylloplane microflora probably reaches its maximum development in tropical rainforest (Ruinen, 1961, 1963, 1965).

1. The Phylloplane Bacteria

Generally the bacteria are the first invaders of the young leaves, and their numbers increase considerably as the growing season progresses. Mangenot (1966*b*) found more than 600×10^6 bacteria per g of *Malus sylvestris* Mill, leaves, and Holm and Jensen (1972) found up to 40×10^6 per g of *Fagus* leaves shortly before leaf fall. In the evergreen tropical rainforest, conditions on the phylloplane are more stable, but a development comparable to that in the deciduous forest can be observed if single leaves are examined at different times from unfolding to senescence. The total numbers of bacteria, however, can reach much higher values than in the temperate regions (Ruinen, 1961).

Usually, the first bacteria to invade newly formed leaves are yellow pigmented rods, and often this type remains dominant throughout the whole development, but as the leaves mature, and senescence begins, a larger number of different species may appear. Lactic acid bacteria are often present together with a variety of non-pigmented, non-spore-forming rods, but the bacterial flora of the phylloplane in temperate regions is especially characterized by the very sparse occurrence of spore-forming bacteria and Actinomycetes (Last and Deighton, 1965; Mangenot, 1966*a*; Jensen, 1971; Holm and Jensen, 1972). In the tropics Actinomycetes seem to be more common in the phylloplane, and a rich flora of nitrogen-fixers is often present (Ruinen, 1961, 1965).

2. *Filamentous Fungi in the Phylloplane*

The first workers to pay attention to the saprophytic fungi on living tree leaves were probably Smit and Wieringa (Smit, 1953; Smit and Wieringa, 1953; Wieringa, 1955) who observed a very regular occurrence of *Aureobasidium pullulans* on leaves of many different deciduous trees and shrubs. They isolated this fungus from very young leaves in the early spring; *A. pullulans* is also the most common filamentous fungus within dormant buds (Davenport, 1966; Pugh and Buckley, 1971*b*). *Cladosporium herbarum* has been isolated from buds (Keener, 1951), and both *A. pullulans* and *C. herbarum* may occur as sooty moulds on twigs and branches (Friend, 1965). Although these fungi are thus present from the unfolding of the leaves, the development of the fungal flora usually seems to lag somewhat behind that of the bacteria, which apparently are better adapted to the conditions on the young leaf.

Pugh and Buckley (1971*a*) found that *A. pullulans* could be isolated from leaves of *Acer pseudoplatanus* L. from the opening of the buds until after the leaves were shed, but direct microscopy of the leaves indicated that active growth was restricted to the first two months. From July onwards it was found only as dark, thick-walled chlamydospores. *C. herbarum* and *Epicoccum nigrum* appeared on the leaves a little later, but continued to grow more or less actively until leaf-fall. *Alternaria* spp. and *Botrytis cinerea* occurred sporadically. Colonization of internal leaf tissue was recorded for *A. pullulans* soon after the opening of the buds and for *C. herbarum* in a few cases in June and more frequently from September onwards. *Epicoccum*, *Alternaria* and *Botrytis* only invaded the interior of obviously senescing leaves.

Hogg and Hudson (1966) made similar studies on *Fagus sylvatica* L. and found that the most important primary colonizers were *Discula quercina* (conidial state of *Gnomonia errabunda*), *Cladosporium herbarum*, *Aureobasidium pullulans*, *Alternaria tenuis* and *Botrytis cinerea*. *D. quercina* was

characterized as the first colonizer of the leaves, being present as mycelium in the green parts of the leaves as early as July. *C. herbarum* was the most abundant primary colonizer, but it only occurred on damaged, necrotic parts of the leaves. The total number of species observed on the leaves reached a peak in October at about the time of the leaf-fall.

Ruscoe (1971) examined the fungal colonization of leaves of *Nothofagus truncata* (Col.) Ckn. in New Zealand and found that the leaves were invaded at a very early stage by parasitic species of *Pestalotia*, *Tubercularia*, *Stachylidium* and *Phoma*, which were all present also after leaf-fall. *A. pullulans* formed vigorously growing colonies, whose development increased with increasing leaf age and then declined at leaf-fall. This species also occurs regularly on leaves of trees and shrubs in the humid tropics (Ruinen, 1963).

3. Yeasts in the Phylloplane

Yeasts are almost always present on the surface of living leaves, and they are amongst the first colonizers, often appearing simultaneously with *Aureobasidium*. Yeasts have also been found in dormant buds by Vosnyakovskaya (1962), Davenport (1966) and Hislop and Cox (1969). The species, which have been isolated and identified, mainly belong to the families Cryptococcaceae and Sporobolomycetaceae. Ascosporogenous yeasts are seldom found in the phylloplane, but it contains a higher percentage of pigmented forms than most other habitats.

Ruinen (1963) examined leaves from tropical trees and shrubs from Indonesia, Africa and South America, and isolated 16 different yeast species. The most important genus was *Cryptococcus* (mainly *C. laurentii* and *C. luteolus*) followed by *Rhodotorula*, while species of *Sporobolomyces* and *Candida* were less numerous. In Denmark the occurrence of yeasts in the phylloplane of *Fagus sylvatica* has been examined, and yeasts were found at all times from unfolding to fall of the leaves. The dominant genus was *Torulopsis* followed by *Sporobolomyces*, while species of *Rhodotorula*, *Cryptococcus* and *Candida* occurred sporadically.

Hogg and Hudson (1966) studied the occurrence of ballistospore-forming yeasts and detected *Sporobolomyces roseus*, *Bullera alba*, *Tilletiopsis minor* and *Itersonilia perplexans*, which all appeared on the leaves soon after unfolding and persisted as surface inhabitants until after leaf-fall. Two species, *S. roseus* and *T. minor*, were encountered with almost 100% frequency, but they did not invade the internal tissues of the leaves. Pugh and Buckley (1971*a*) found *Sporobolomyces* commonly on *Acer pseudoplatanus*, especially on the upper surface of the leaves. It began to appear in May and increased considerably during the following months, Ruscoe (1971) also found *Sporobolomyces* on *Nothofagus truncata* leaves of all ages, but it was

most common on actively growing leaves, decreasing in abundance at senescence.

4. Activity of the Phylloplane Microflora

All the above-mentioned phylloplane micro-organisms are chemo-organotrophic forms requiring organic nutrients for growth. A certain part of their nutritional needs may be covered by organic substances from the atmosphere, adsorbed or deposited on the surface of the leaves. The bulk of the organic nutrients, however, must be derived directly or indirectly from the leaves on which the organisms live. Possible sources are leaf exudates, honeydew and faecal material from the leaf fauna, dead or necrotic parts of the leaves, and healthy leaf tissue. It is hardly possible to distinguish in detail between the utilization of these different nutritional sources, but it seems natural to assume that leaf exudates and healthy leaf tissues are the most important sources on young leaves, whereas animal products and dead tissues become more important as the leaves mature and senesce. The availability of different types of nutrients at different stages of leaf development is probably the main factor determining the succession of micro-organisms on the leaves.

Apart from the pathogenic forms, the phylloplane bacteria do not invade the healthy tissue, and their most probable sources of nutrients are leaf exudates, faecal material, and metabolic products from the leaf fungi. Among the fungi several of the primary colonizers are host-specific or host-restricted weak parasites, which can utilize the living leaf tissue, often without causing visual disease symptoms (Hudson, 1968). *Aureobasidium* can also grow internally in healthy leaves, especially in vascular tissue. It is known to be pectinolytic, but it does not normally cause necrosis. Other fungi, such as *Cladosporium* and *Epicoccum*, are only able to invade damaged or senescent leaf tissue, and others again, such as *Sporobolomyces*, grow exclusively on the leaf surface.

Ruinen (1966) has shown that several of the common phylloplane yeasts are able to attack the leaf cuticle by decomposing the cutin, and many of them could also decompose pectin slightly. This damage to the leaf cuticle results in increased permeability of the leaf surface, so that greater amounts of nutrients may be secreted or leached from the leaf.

It is not possible to evaluate exactly the effects of the microbial activity on and in the leaves in the tree canopy. A consequence, however, must be that a certain proportion of the photosynthetic products formed by the leaves is utilized by the micro-organisms, and that the decomposition of the leaves themselves is already well under way when they reach the ground after leaf-fall. It is also highly probable that leaf senescence is accelerated by microbial activity.

B. Animal Activity in the Canopy

Simultaneously with the microbial activity in the tree canopy the leaves are also attacked by primary consumers in the form of phytophagous insects or insect larvae. The most important foliage-feeding insects belong to the orders Hymenoptera, Coleoptera, and Lepidoptera, but foliage feeders are also found within the orders Orthoptera, Diptera, and Hemiptera (Franklin, 1970). In general, the feeding habits of these insects can be classified into sap sucking, leaf chewing, skeletonizing, and leaf mining.

The types of leaf consumption, which result in visible loss of leaf tissue, measurable in terms of leaf area, can be quantitatively estimated by examination of either the attached leaves in the canopy or the fallen leaf litter. Rothacker *et al.* (1954) examined five stands of mixed oak in Tennessee and found that in the early season an average of 3·7% of the foliage was dead or eaten by insects. By midsummer this percentage had increased to 5·4, and by late season to 6·7.

Three forest stands in southern Ontario, Canada, have been studied by Bray (1964), who determined the area of attached tree leaves utilized by primary consumers. Mean yearly utilization over a three-year period was 10·6% for a xeric *Quercus* forest, 6·6% for a mesic *Acer–Fagus* forest, and 5·9% for a moist *Acer-Fagus* forest. Reichle and Crossley (1967) found in a forest stand in Tennessee, dominated by *Liriodendron tulipifera* L., an average consumption by insects of 5·6% of the total leaf area, determined just before leaf fall. In Denmark the primary consumption in the canopy of a stand of *Fagus sylvatica* has been studied over a five-year period (Nielsen, in press). The yearly averages varied from 6·8% to 17·1% and the average of the whole period was 12·2%.

Occasionally, populations of leaf-eating insects may develop to such a degree that total defoliation occurs. Under normal conditions, however, most occur in comparatively small numbers, and the level of primary consumption in the tree canopy seems normally to vary within rather narrow limits. A consequence of the animal activity in the canopy is that a certain part of the leaf tissue, often 5–15%, is mechanically disintegrated and falls to the ground as insect frass, which is more easily decomposed than the intact leaves by litter micro-organisms. In addition, the attack on leaves in the canopy accelerates microbial activity by creating favourable conditions for those micro-organisms that grow in damaged or dead leaf tissue or in faecal material.

C. Leaching of Nutrients from the Canopy

Reviews covering the literature on leaching from plants have been published recently by Tukey (1970, 1971). Tukey and Morgan (1962) list 8

carbohydrates, 10 organic acids, 16 amino acids, and 13 inorganic compounds, which have been demonstrated in plant leachates. Information about the total amounts of organic substances leached from tree canopies under natural conditions is sparse, but the few figures published indicate that these amounts can be rather large. Most of the organic substances in leachates probably are soluble carbohydrates (Dalbro, 1955), and Carlisle *et al.* (1966*b*) found that the carbohydrate in rainwater collected under a *Quercus* canopy mainly consisted of melezitose, a trisaccharide found in honeydew, indicating that these organic substances are not necessarily leached directly from the leaf tissue, but may be deposited first on the leaf surface by sap-sucking aphids.

Much more information is available with regard to the inorganic compounds in plant leachates. The data recorded in Table I indicate that inorganic substances, especially potassium, can also be leached in considerable amounts, and that the leached amounts are much higher in tropical than in temperate regions, again especially with regard to potassium. Different tree species differ as to degree of leaching, and the loss by leaching also depends upon the age of the leaves, and upon microbial or animal attack. A greater loss of nutrients generally occurs from older than from younger leaves, and microbial attack on the leaf cuticle increases both wettability and permeability of the leaf surface, leading to increased leaching (Tukey and Morgan, 1962; Ruinen, 1966).

A comparison between the amounts of plant nutrients leached from the canopy and the amounts added to the soil in the litter-fall (Table IV) shows that the nutrients in the leachates play an important part in the total circulation of minerals in the ecosystem. The influence of this more or less continuous addition of easily decomposable organic substances and inorganic nutrients on the decomposition processes in the litter layer is difficult to evaluate quantitatively, but it undoubtedly must have a considerable stimulatory effect on the microbial activity.

III. The Litter Fall

Since the classic work of Ebermayer (1876) a vast amount of literature concerning litter fall in forest stands has accumulated. The subject is discussed in detail by Lutz and Chandler (1946) and Aaltonen (1948), and a very comprehensive review of the literature up to 1964 is given by Bray and Gorham (1964). Most of the early work was done on forest stands in the temperate zone of the northern hemisphere, but during recent years a considerable number of studies have been carried out in other parts of the world.

TABLE I. Leaching of nutrients from the tree canopy

		kg ha^{-1} year					
		N	P	K	Ca	Mg	Organic matter
Malus domestica Borkh., Denmark (Dalbro, 1955)	T	—	—	29·2	14·3	—	—
	L(T − I)	—	—	27·5	10·5	—	>1000
Hardwood plantations, England (Madgwick and Ovington, 1959)	T	—	—	27·8	24·5	11·0	—
	L(T − I)	—	—	25·0	13·8	6·8	—
Fagus sylvatica, Denmark (Nielsen, in press)	T	—	1·40	16·76	12·00	5·69	—
	S	—	0·21	4·28	1·67	0·95	—
	L(T + S − I)	—	0·19	10·14	0·50	2·38	—
Mixed oak wood, Belgium (Denayer-de Smet, 1969)	T	10·5	—	23·4	27·0	—	—
	S	0·9	—	2·0	3·2	—	—
	L(T + S − I)	1·0	—	20·2	12·6	—	—
Quercus petraea, England (Carlisle *et al.*, 1966*b*)	T	8·82	1·31	28·14	17·18	9·36	453
	L(T − I)	−0·72	0·88	25·18	9·88	4·73	349
Quercus ilex, France (Rapp, 1969*a*)	T	19·1	3·0	31·0	32·1	4·8	—
	L(T − I)	3·6	2·6	28·7	19·6	3·5	—
Tropical rainforest, Ghana (Nye, 1961)	T	26·4	4·10	237·3	41·6	29·1	—
	L(T − I)	12·4	3·79	219·8	28·9	17·8	—

I = incident precipitation S = stem flow T = throughfall L = leachate

A. Litter Fall Patterns

The pattern of litter fall varies greatly throughout the different climatic zones. In deciduous stands in the cool temperate zone of the northern hemisphere the leaf fall is normally concentrated in a rather short autumnal period, often with a pronounced peak in October or November (Viro, 1955; Witkamp and van der Drift, 1961; Carlisle *et al.*, 1966*a*; Duvigneaud *et al.*, 1969; Andersson, 1970). In a mixed oak forest (*Quercus ellipsoidalis* E. J. Hill and *Q. alba* L.) in Minnesota, U.S.A., Reiners and Reiners (1970) found that 20% of the litter fell in September, 50% in October, 9% in the 5 winter months, and 21% (probably flowers, bud scales, etc.) in April–August. As another example it can be mentioned that in a 90-year-old stand of *Fagus sylvatica* in Denmark, 82–88% of the leaf fall occurred in October and November. Bud scales and flowers fell mainly in May and June, and fruits in September and October, whereas fall of dead twigs and branches occurred more or less evenly throughout the year (Nielsen, in press).

In the evergreen *Quercus ilex* L. woodlands in southern France the leaves have a life span of about 2 years, and they are shed mainly in the period from April to June with a peak in May (Rapp, 1969*b*). Likewise, in the evergreen stands of *Nothofagus truncata* in New Zealand the main leaf fall occurs in the early summer, mid-September to mid-November, coincident with the development of new leaves (Miller, 1963). The warm temperate forests of eastern Australia show a very similar pattern, whereas *Eucalyptus* forests in Victoria and western Australia deposit leaf litter mainly in the warm, dry part of the year (Bray and Gorham, 1964).

In the dry tropical region of West Africa (Senegambia) Jung (1969) observed that *Acacia alba* shed its leaves during the rainy season in August and September, whereas in humid equatorial forests litter fall is more or less continuous throughout the year, although with a tendency for extensive falls during or shortly after relatively dry periods. Thus, Laudelot and Meyer (1954) found that litter fall at Yangambi (Congo) was low during the rainy seasons and reached a peak at the end of the dry seasons. Nye (1961) found in the moist tropical forests of Ghana a relatively high litter fall during February and March due to a short dry season in January and February. Madge (1965) and Hopkins (1966), both working in Nigeria, found that maximum leaf fall occurred during the dry-season months of November to March. The former stated that the leaf fall fluctuated little during the wet season, but at the start of the dry season it progressively increased, culminating during the driest month, and then falling off again. A similar pattern is found in south-east China in forests dominated by *Gironniera subaequalis* (Rodin and Bazilevich, 1967). Here the leaves fall all

the year round, but with a peak period from March to May, where March–April is the dry season and the wet period starts in May.

B. Annual Amounts of Litter

Table II contains a number of examples of the annual amounts of litter falling in forest stands of the more important broad-leaved tree species in the different climatic zones of the world (see Williams and Gray, Chapter 19). The most important part of the litter material is the leaf litter, and the

TABLE II. Annual amounts of litter fall

Dominant tree species or forest type	Locality	Litter fall (t ha^{-1} year)		Reference
		Leaf litter	Total litter	
COOL TEMPERATE REGION				
Acer saccharum Marsh.	Quebec, Canada	2·17–3·62	—	Maldague, 1967
Alnus rubra Bong.	Oregon, U.S.A.	3·64–6·39	4·49–9·90	Zavitkovski and Newton, 1971
Betula populifolia Marsh.	Eastern Canada	1·03–2·34	—	Coldwell and DeLong, 1950
Betula spp.	Finland	0·94–1·27	1·50–1·80	Viro, 1955
Fagus grandifolia Ehrh.	Eastern Canada	1·69–2·10	—	Coldwell and DeLong, 1950
Fagus sylvatica	South Sweden	3·57	5·70	Nihlgard, 1972
Fagus sylvatica	Denmark	2·79	3·94	Nielsen, in press
Populus spp.	Eastern Canada	1·00–2·04	—	Coldwell and DeLong, 1955
Populus spp.	Voronezh, U.S.S.R.	—	4·6–6·0	Sviridova, 1961
Quercus petraea	England	2·13	3·86	Carlisle *et al.*, 1966*a*
Quercus robur	South Sweden	3·26	5·28	Andersson, 1970
Mixed hardwood	New York, U.S.A.	2·72–3·38	—	Chandler, 1941
WARM TEMPERATE REGION				
Eucalyptus regnans	Victoria, Australia	3·6–4·2	6·9–8·1	Bray and Gorham, 1964
Eucalyptus diversicolor	Western Australia	2·7–2·8	5·7–6·0	Stoate, 1958
Nothofagus truncata	New Zealand	2·14–6·91	3·27–8·85	Miller and Hurst, 1957
Quercus ilex	Southern France	2·45–2·72	3·84–7·00	Rapp, 1969*b*
Quercus coccifera	Southern France	1·41–1·58	2·28–2·61	Rapp, 1969*b*
Evergreen mixed stand	Japan	6·88	9·25	Kitazawa, 1967
TROPICAL REGION				
Gironniera subaequalis	South-east China	—	5·80	Rodin and Bazilevich, 1967
Acacia alba	Senegambia	2·50	11·50	Jung, 1969
Tropical rainforest	Nigeria	3·70	5·60	Madge, 1965
	Ghana	7·00	10·50	Nye, 1961
	Congo	—	12·30–15·30	Laudelot and Meyer, 1954
	Columbia	—	8·52–10·11	Jenny *et al.*, 1949
	Malaya	—	5·5–14·8	Bray and Gorham, 1964
	Thailand	11·9	23·3	Kira and Shidei, 1967

importance of other litter components has not always been appreciated. It is not quite clear in some of the older literature whether the data represent total litter or only leaf litter, and this detracts from the value of these earlier data.

One of the factors, which might be expected to affect the amounts of litter fall in a forest stand, is the species composition. A comparison of the data, however, indicates that differences between tree species are rather small. When sites, similar with regard to soil type and climatic conditions, are compared, the variation within a single species may be almost as large as the variation between the different species growing on these sites (Lutz and Chandler, 1946). The age of the trees is important only in very young stands. Here the amount of litter increases with increasing age, until the canopy becomes closed, and then the annual litter fall tends to remain fairly constant over a long period of time (Møller, 1945; Bray and Gorham, 1964; Zavitkovski and Newton, 1971).

The influence of soil fertility was studied by Chandler (1941), who compared the litter fall in mixed hardwood stands in central New York State, U.S.A. A statistically significant difference was found between "productive" and "unproductive" sites, but it is emphasized that the difference was small, and that one should not expect large differences in litter fall due to differences in site quality. Møller (1945) compared leaf fall in a large number of Danish *Fagus sylvatica* stands belonging to different site classes, and he failed to find any significant site influence on the production of leaf litter. Similarly, Handley (1954) reached the conclusion that probably no difference exists between mull and mor with regard to litter production on otherwise similar sites. On the other hand, Scott (1955) expressed the opinion that the annual litter fall is quite closely correlated with the general productivity of the site. However, this seems to be true mainly in cases where variations in general productivity are determined by differences in the local climate and not by differences in the nutritional status of the soil.

Climate, including effects of altitude and exposure, seems to be by far the most important factor, determining the annual amounts of litter produced in forest stands. A striking example of this is given by Mork (1942), who examined two *Betula* stands, one at an altitude of 180 m and the other at 800 m above sea-level, and found a total litter fall of 1876 kg ha^{-1} and 799 kg ha^{-1} respectively. Bray and Gorham (1964) have also demonstrated the influence of climate by comparing data from the major climatic zones. They found that total litter production averages 1 t ha^{-1} year in arctic-alpine forests, 3·5 t ha^{-1} year in cool temperate forests, 5·5 t ha^{-1} year in warm temperate forests, and 11 t ha^{-1} year in equatorial forests (cf. Table II).

C. Composition of the Litter

As mentioned above, the non-leaf components of the litter have been almost or wholly neglected in many of the older studies, but during recent years a number of rather detailed analyses of litter material have been published (Table III). It is characteristic of these recent results that the percentages of non-leaf material quoted are considerably higher than in most previous studies. Among the data presented by Bray and Gorham (1964) similar results are found only for *Eucalyptus* stands in Australia, where bark fall is especially high. The mean percentage of non-leaf litter from angiosperms is stated to be 21% in cool temperate climates and 23% and 42% in warm temperate climates in North America and Australia respectively. Probably, the amounts of non-leaf material have often been greatly underestimated.

Møller (1945) made the interesting observation that the production of dead twigs and branches increases with increasing general productivity of *Fagus* stands, whereas leaf fall remains almost constant. Consequently, twigs and branches will constitute a higher percentage of the total litter material on productive than on non-productive sites, and this may influence the physical structure of the litter layer. Normally, the increased admixture of twigs and branches will improve the structure in favour of the decomposer organisms.

The concentration of plant nutrients in litter material is important because of its influence both on the rate of decomposition of the litter and on the amounts of nutrients liberated during the decomposition, Here again, interest has in the past been concentrated mainly on the leaf fraction, and numerous results of chemical analyses of leaf litter have been published, whereas corresponding figures for the non-leaf material are scarce. However, serious underestimates of the total amounts of nutrients added to soil through litter fall may result if the non-leaf material is disregarded (Carlisle *et al.*, 1966*a*). Analytical data of leaf litter or total litter from a large number of different tree species are given by Melin (1930), Broadfoot and Pierre (1939), Wittich (1953) and Scott (1955) and data from several other sources are reviewed by Lutz and Chandler (1946), Aaltonen (1948), Handley (1954), Bray and Gorham (1964), and Remezov and Pogrebnyak (1969). Some examples are recorded in Table IV. Detailed analyses (Table V) of the different litter components have been carried out by Carlisle *et al.* (1966*a*), Duvigneaud *et al.* (1969) and Jung (1969).

With regard to total ash content of angiosperm tree leaf litter Bray and Gorham (1964) distinguish between Fagaceae, usually containing 4–8% ash (average of 13 species, 6·3%), and non-fagaceous angiosperms, usually containing 8–14% ash (average of 43 species, 10·4%). They state that ash

TABLE III. Components of litter fall (see also Williams and Gray, Chapter 19)

	1		2		3		4		5		6	
	W	%	W	%	W	%	W	%	W	%	W	%
Leaves	2127	55·13	3047	58·58	2585	47·69	2713	67·04	3139	49·86	2500	21·7
Bud scales	192	4·98			—	—	303	7·49	232	3·61	—	—
Flowers	150	3·89	405	7·79	1687	31·13	84	2·08	116	1·81	1700	14·8
Fruits	52	1·35					534	13·19	249	3·88	5400	47·0
Twigs and branches	1163	30·14	1234	23·73	1148	21·18	413	10·21	1991	30·99	1900	16·5
Miscellaneous material	174	4·51	515	9·90	—	—	—	—	698	10·86	—	—
Total non-leaf litter	1732	44·89	2154	41·42	2835	52·31	1334	32·96	3286	51·14	9000	78·3
Total litter	3858	100	5201	100	5420	100	4047	100	6425	100	11500	100

1: *Quercus petraea*, England (Carlisle *et al.*, 1966*a*).
2: *Quercus robur*, Sweden (Andersson, 1970).
3: *Quercus ilex*, France (Rapp, 1969*b*).
4: *Fagus sylvatica*, Denmark (Nielsen, in press).
5: Mixed deciduous stand, Belgium (Duvigneaud *et al.*, 1969).
6: *Acacia alba*, Senegambia (Jung, 1969).
W = kg dry wt ha^{-1} year.

TABLE IV. Total amounts of nutrients returned annually to the soil in the litter fall

Dominant tree species or forest type	kg ha^{-1} year					Reference
	N	P	K	Ca	Mg	
Betula spp.	30–34	7·9–9·2	22·4–26·6	24·9–47·7	11·4–14·2	Remezov and Pogrebnyak, 1969
Alnus rubra	30·9	1·7	13·0	—	—	Tarrant, 1964
Alnus rubra	112·3	—	—	—	—	Tarrant *et al.*, 1969
Quercus ilex	32·8–87·5	2·82–9·61	16·2–38·5	63·9–121·8	4·56–10·33	Rapp, 1969b
Quercus petraea	41·06	2·19	10·51	23·83	3·87	Carlisle *et al.*, 1966a
Quercus spp.	35–40	8·4–12·3	15·8–18·3	66·0–78·1	10·7–12·8	Remezov and Pogrebnyak, 1969
Mixed *Quercus* forests	50–77	2·3–6·2	21·0–31·5	77–110	5·6–9·7	Duvigneaud *et al.*, 1969
Fagus sylvatica	69	5·0	14·4	31·7	4·3	Nihlgård, 1972
Fagus sylvatica	33·5	1·7	8·5	33·4	5·18	Nielsen, in press
Nothofagus truncata	37	2·5	9	71	11	Miller, 1963
Populus spp.	31–54	3·5–4·4	22·4–84·7	66·0–105·1	9·9–14·2	Remezov and Pogrebnyak, 1969
Mixed hardwood	18·6	3·7	15·1	73·5	10·3	Chandler, 1941
Tropical rainforest	140–224	4–9	48–104	84–124	43–53	Laudelot and Meyer, 1954
Tropical rainforest	178	6·5	61	184	40	Nye, 1961

(— means not determined)

TABLE V. Concentrations of nutrient elements in different litter components

		kg ha^{-1} year				
		N	P	K	Ca	Mg
Quercus petraea (Carlisle *et al.*, 1966*a*)	Leaves	21·05	0·92	6·30	16·77	2·74
	Bud scales	3·08	0·20	0·46	1·08	0·15
	Flowers	4·31	0·31	1·24	0·68	0·24
	Fruits	0·44	0·03	0·19	0·23	0·04
	Twigs and branches	7·73	0·39	1·58	4·18	0·53
	Miscellaneous	4·45	0·34	0·74	0·89	0·17
	Total	41·06	2·19	10·51	23·83	3·87
Mixed oakwoods (Duvigneaud *et al.*, 1969)	Leaves	32·1	2·4	13·5	55·5	5·1
	Bud scales	3·6	0·3	0·9	2·1	0·3
	Flowers	3·8	0·3	1·1	1·2	0·3
	Fruits	1·6	0·1	2·0	0·3	0·1
	Twigs and branches	14·1	0·7	3·7	25·5	1·5
	Miscellaneous	9·1	0·7	5·3	6·8	0·8
	Total	64·3	4·5	26·5	91·4	8·1
Acacia alba (Jung, 1969)	Leaves and flowers	89·3	1·2	17·3	99·0	23·2
	Fruits	71·8	2·3	53·4	22·7	5·9
	Wood and bark	25·4	0·4	4·9	100·3	9·7
	Total	186·5	3·9	75·6	222·0	38·3

content is usually low in taxa which often occur on more infertile sites and as pioneers in forest development, whereas there is a higher ash content in taxa which normally occur on fertile soils and in more developed (climax) forest communities. This is in good agreement with the observation by Handley (1954) that litter of tree species usually associated with mor sites generally has rather low contents of mineral elements, as compared to litter of species normally growing on mull sites.

Information on the chemical composition of the organic fraction of litter is rather scanty because of technical difficulties in the separation and determination of the different constituents. Crude proximate analyses have been carried out according to various modifications of the Waksman method (Melin, 1930; Ohmasa and Mori, 1937; Wittich, 1943; Coldwell and

DeLong, 1950; Handley, 1954; Mikola, 1954). This kind of analysis of angiosperm leaf litter has given results within the following ranges: water-soluble substances, 6–27%; alcohol-soluble substances, 3–13%; ether-soluble substances, 4–12%; "hemicelluloses", 11–26%; cellulose, 6–22%; "lignin", 16–42%; "crude protein", 2–16%. The data are too sparse to allow generalizations with regard to differences between tree species.

More detailed analyses of the water-soluble components have been carried out by Nykvist (1963), and determinations of the concentration of tannins (polyphenols) have been published by several authors (Coulson *et al.*, 1960; Heath and King, 1964; King and Heath, 1967; Satchell and Lowe, 1967; Feeney and Bostock, 1968) because of the possible influence of these substances on the decomposition processes. Calorific values for litter material have been published by Bocock (1964), Carlisle *et al.* (1966*a*), White (1968), Reiners and Reiners (1970) and others, and some examples of the results are recorded in Table VI. The data do not allow any generalizations with regard to differences between tree species or different litter components, but at least there do not seem to be any big differences. Most of the values fall within the range of 4·5–5·0 kcal g^{-1} dry matter.

IV. Decomposition Processes in the Litter Layer

A. The Litter Microflora

1. The Bacterial Flora of Litter

When samples of freshly fallen litter are incubated in the laboratory under adequate moisture and temperature conditions, the bacterial numbers usually show a strong increase during the initial stages of the experiment, correlated with an increase in pH and a disappearance of soluble organic components. Often a peak in numbers is reached within a few weeks, and then the numbers gradually decrease again. Litters with an initially high pH show the most rapid increase and reach the highest maximum numbers, which may be as high as 10^9–10^{10} per g dry matter (Marten and Pohlman, 1942; Mangenot, 1966*b*).

Under natural conditions in the litter layer the bacterial flora usually develops more slowly than in laboratory experiments, partly due to the lower temperature and because unfavourable weather conditions cause discontinuities in the development, but similar trends to the laboratory experiments have been observed. Thus, Witkamp (1960) and Minderman and Daniëls (1967) determined bacterial numbers in litter collected from a calcareous mull site in Holland at different times after leaf fall. In both cases maximum numbers were found a few weeks after shedding of the leaves, and this was followed by a gradual decrease.

Similar examination have been carried out in a mixed oak wood in Belgium (Remacle, 1970, 1971), and in stands of *Fagus sylvatica* in Germany (Meyer, 1960) and Denmark (Holm and Jensen, 1972). In the latter

TABLE VI. Calorific value of litter material

Tree species	kcal g^{-1} dry wt	References
ANNONACEAE		
Asimina triloba (L.) Dunal	4·63	5
SALICACEAE		
Populus grandidentata Michx.	5·06	4
BETULACEAE		
Alnus glutinosa (L.) Gaertn.	5·08	1
Alnus incana (L.) Moench.	4·93	3
Alnus rugosa (Duroi) Spreng	4·60	4
Betula alba L.	4·82	3
Betula lutea	4·52	4
Betula papyrifera	4·87	4
Betula pubescens and *B. verrucosa*	4·72	2
FAGACEAE		
Fagus sylvatica	4·52	3
Nothofagus obliqua	4·46	3
Castanea sativa Mill.	4·69	3
Quercus alba L.	4·47	4
Quercus ellipsoidalis	4·78	4
Quercus petraea	4·61–4·94	1, 2, 3
Quercus robur	4·71	3
Quercus rubra L. sec. Duroi	4·72	3
ULMACEAE		
Ulmus americana L.	4·26	4
ACERACEAE		
Acer rubrum L.	4·43	4
OLEACEAE		
Fraxinus excelsior L.	4·51	1
Fraxinus nigra Marsh.	4·37	4

1: Bocock, 1964; 2: Carlisle *et al.*, 1966*a*; 3: Ovington and Heitkamp, 1960; 4: Reiners and Reiners, 1970; 5: White, 1968.

case no consistent trends with regard to seasonal variation could be observed. Apparently, the bacterial numbers here were affected more by the changing weather conditions than by the age of the litter. In Japan, Saito

(1956) determined the numbers of bacteria at different depths of the forest floor under a stand of *Fagus crenata*. The lowest number was found in the L layer, and the highest in the middle of the F layer, while at greater depths the number again decreased.

Witkamp (1963, 1964, 1966) compared the numbers of bacteria in leaf litter from different tree species, growing under different environmental conditions, in Tennessee, U.S.A. The numbers tended to be highest in spring, and they were higher at low than at high altitudes, but the dominant factor controlling bacterial density was the tree species. As might be expected, more easily decomposable leaf species with low C:N ratios harboured higher numbers of bacteria than did more resistant leaf species, especially in freshly fallen litter. With progressive decay the influence of the tree species decreased, and environmental influences increased.

Few studies have been carried out on the composition of the bacterial flora in litter. Mangenot (1966*b*) found that the bacterial flora on freshly fallen *Malus* leaf litter mainly consisted of yellow or orange pigmented forms as in the phylloplane. During laboratory incubation, the percentage of the pigmented forms diminished, while Actinomycetes, which were initially absent, began to appear after 20 days and constituted about half the bacterial flora after 180 days.

Remacle (1971) studied the bacterial flora of *Quercus* leaf litter collected from the litter layer of a Belgian oak wood at different times during the period from December till June. Species of *Flavobacterium* and *Achromobacter* occurred frequently during the whole period. *Pseudomonas* spp. were common in December and January, but disappeared completely in April and June. *Bacillus* spp. occurred apparently at random in some months, not in others. *Streptomyces* spp. were absent from December until February, but appeared sparsely in March, April and June. A similar examination was carried out by Holm and Jensen (1972) on *Fagus* litter, and they found a bacterial flora very similar in composition to that on the mature leaves in the canopy. Yellow pigmented forms were numerous, although the percentage was somewhat lower than in the canopy, and spore-formers and Actinomycetes were rare (Table VII). No consistent trend with regard to seasonal changes in the composition was observed.

In summary, the development of the bacterial flora after litter fall can be depicted as follows: initially a considerable increase in bacterial numbers occurs, owing to improved moisture conditions but apparently without any great changes in the species composition. It seems mainly to be the bacteria already present on the senescent leaves that start to multiply profusely. In litter that is easily decomposable the numbers may reach very high values in a short time, and then they decrease gradually. In more resistant litter the development is slower, and the number may increase gradually over a

long period. Thereby an initially large difference between different types of litter is diminished as decomposition progresses. During the later stages of decomposition the litter may be invaded by soil bacteria, not commonly present in the phylloplane, especially Actinomycetes and spore-formers.

TABLE VII. Composition of the bacterial flora in canopy, litter and surface soil of a Danish *Fagus* forest

	Numbers per g dry $\times 10^{-6}$	Percentage distribution					
		Spore-forming rods	Non-spore-formers				
			Pigmented rods	Non-pigmented rods	*Arthrobacter* like rods	Actinomycetes	Miscellaneous
Canopy							
spring	1·95	1·5	46·5	36·4	5·9	0·7	9·0
autumn	17·56	0·8	44·8	21·1	12·6	0·9	19·8
Litter layer	720	0·8	30·6	35·8	17·3	1·5	14·0
Surface soil	26·9	21·2	5·6	21·9	18·2	18·8	14·3

All figures are average values from a considerable number of experiments during the years 1968–1971 (adapted from Holm and Jensen, 1972).

2. *Filamentous Fungi in the Litter Layer*

The fungal flora of litter material has been studied to a far greater extent than the bacterial flora, but in contrast to the bacteriological studies the mycological studies have mainly been of a qualitative nature, a natural consequence of the methodological problems involved in quantitative measurements of fungi in plant material. The use of dilution plate counts for this purpose has been seriously questioned, because the colonies on the plates mainly develop from spores. The colony numbers, therefore, give no direct information about the amount of fungal mycelium in the sample examined. However, the plate count also has its advocates. Witkamp (1966) presented data which suggest that plate counts quantitatively reflect the entire microflora, and he claimed that failure of the method may have been the result of too few sampling periods, and that year-round samples make the method successful.

In laboratory incubation experiments the fungal counts generally follow a pattern similar to that of the bacterial counts with an initial increase to a

maximum after a few weeks followed by a gradual decrease (Marten and Pohlman, 1942; Mangenot, 1966*b*).

In the litter layer of stands of *Fagus sylvatica* in Germany, Meyer (1960) found fungal counts from 0·9 to 3·4 $\times$ 10^6 g^{-1} organic matter, with the lowest count on the most productive soil type. The ratio between bacterial and fungal counts varied from 22:1 on the most productive soil to 0·9:1 on an infertile iron-podsol soil. In a Danish stand of *Fagus sylvatica*, growing on a fertile mull soil, fungal counts in the litter layer averaged about 10 $\times$ 10^6 g^{-1} dry weight without signs of any regular seasonal variation, and the average ratio between bacteria and fungi was 89:1.

Witkamp (1960, 1963, 1964, 1966) counted both bacteria and fungi in litter from several different tree species in Holland and North America. The differences between tree species with regard to fungal counts were smaller and less consistent than with regard to bacterial counts, but the ratio between bacteria and fungi appeared to be positively correlated to the rate of decomposition of the litter. The ratio was higher for more easily decomposable litter than for more resistant litter, and higher under environmental conditions favouring a rapid decomposition than under more adverse conditions, which is in good agreement with the observations in Germany (Meyer, 1960).

A few attempts have been made to determine the amounts of fungal mycelium in litter by means of methods involving direct microscopy. Minderman and Daniëls (1967) examined the litter layer of a young stand of *Quercus robur* L. in Holland. They found no mycelium on the freshly fallen litter, but from the middle of November fungi rather suddenly appeared in considerable quantity, rapidly increasing to a relatively steady level of about 1000 m mycelium per g dry organic matter on two mull sites and about 2000 m on a mor site. Nagel-de Boois and Jansen (1971) found in a 135-year-old stand of *Quercus petraea* (Mattuschka) Liebl. mixed with *Fagus sylvatica*, also in Holland, about 2000 m mycelium per g dry weight of the litter layer. In a Danish stand of *Fagus sylvatica*, about 90 years old, much smaller amounts of mycelium have been found, from 151 to 446 m g^{-1} dry weight of litter. The lowest value was found in March and the highest in May. The ratio between plate counts and direct measurements of mycelium on identical samples varied from 15,000 to 74,000 colonies per m mycelium.

Extensive qualitative studies on the fungal populations in tree litter have been carried out using a variety of methods, including isolations from dilution plates and from unwashed, washed or surface-sterilized litter fragments, direct observation of the development of fungi on litter material incubated in moist chambers, and collection of spore deposits from litter suspended over nutrient agar plates. Each of these methods yields

information about a certain section of the fungal populations, and a fairly complete picture of the total mycoflora can only be obtained by piecing together information obtained by different techniques.

Witkamp (1960) found by isolations from dilution plates and leaf discs from freshly fallen litter of *Quercus robur* in Holland a dominant flora of Sphaeropsidales, which disappeared in the course of a few weeks, being mainly replaced by *Cladosporium herbarum*. *Aureobasidium pullulans* was also isolated frequently, whereas species of *Mucor* and *Trichoderma* were rare. From older litter a larger number of genera were isolated, including *Mucor*, *Mortierella*, *Trichoderma*, *Aspergillus*, *Penicillium* and *Alternaria*.

In England the mycoflora of litter in a mixed oak wood has been studied by Hering (1965) by direct examination, damp-chamber incubation and isolation from washed fragments. A large number of species was recorded, and the isolation results agree rather well with the findings of Witkamp. The dominant fungi in fresh litter (0–6 months) were *Aureobasidium pullulans* and species of *Phoma*, *Phomopsis*, *Coleophoma*, *Cladosporium*, *Epicoccum* and *Polyscytalum*, whereas 1–2-year-old litter was dominated by species of *Mucor*, *Penicillium* and *Trichoderma*. In addition, a number of pycnidial and perithecial fungi were recorded on the fallen leaves, mainly species of *Mycosphaerella*, *Venturia*, *Gnomonia*, *Phyllosticta* and *Didymella*, and a great variety of sterile forms, mostly dark-coloured, was obtained both from isolation plates and from damp chambers.

In mixed *Quercus* stands in Belgium abundant occurrence of perithecial fungi, especially *Mycosphaerella* spp., has been recorded on the leaves soon after leaf fall (Froment and Mommaerts-Billiet, 1969; Mommaerts-Billiet and Froment, 1969) and Remacle (1970, 1971) has made a more detailed study of the development of the fungal populations on the litter from leaf-fall till May–June the following year. The dominant types were *Aureobasidium pullulans* and species of *Cladosporium*, *Penicillium*, *Trichoderma*, and *Mucor*. *Aureobasidium* was most common in the beginning and tended to disappear later, whereas the remaining species occurred frequently throughout the period of observation. Other species appeared sporadically.

According to Saito (1956, 1966) the litter of *Fagus crenata* prior to leaf fall harboured a number of fungal species such as *Aureobasidium pullulans*, *Tripospermum myrti*, *Fusarium* sp. and hyaline and dark sterile mycelia. These fungi tended to disappear after leaf fall and were replaced by *Absidia glauca*, *Mortierella ramanniana*, *Penicillium lapidosum*, *P. raistrickii*, *Trichoderma viride* and *Cladosporium herbarum*. Later, 8–10 months after leaf fall, fruit bodies of a Discomycete, *Dasyscypha* sp., were found frequently on the dead leaves, and still later the leaves were invaded by litter-decomposing Hymenomycetes, *Collybia* spp. and *Mycena* spp.

The succession of microfungi on litter of *Fagus sylvatica* has been

studied by Hogg and Hudson (1966). They divided the observed fungal species into three groups. Group 1 fungi: *Discula quercina* (conidial state of *Gnomonia errabunda*), *Cladosporium herbarum* (conidial state of *Mycosphaerella tassiana*), *Aureobasidium pullulans* (conidial state of *Guignardia fagi*), *Alternaria tenuis* and *Botrytis cinerea*; these were already present before leaf fall and persisted in the fallen litter over the winter. Group 2 fungi: *Discosia artocreas*, *Gnomonia errabunda*, *Mollisina acerina*, *Mycosphaerella tassiana*, *M. punctiformis*, and *Guignardia fagi*; these began to sporulate in the late autumn of the year of leaf fall and attained high frequencies in the following spring, and they persisted until the second winter after leaf fall. Group 3 fungi: *Polyscytalum fecundissimum*, *Spondylocladiopsis cupulicola*, *Microthyrium microscopicum*, *Mollisina* sp., *Lachnella villosa*, *Helotium caudatum*, *Endophragmia stemphylioides*, *E. catenulata*, *E. laxa*, *Pistillaria pusilla*, *Chalara cylindrosperma* and *Doratomyces stemonitis*; these appeared in late summer, almost a year after leaf fall. They reached a maximum in the spring and persisted over winter until the following spring.

Novak and Whittingham (1968) examined the litter mycoflora in a mixed (maple-elm-ash) forest in Wisconsin, U.S.A., and recorded 161 different fungal species. The prevalent forms were *Alternaria tenuis*, *Aureobasidium pullulans*, *Cladosporium herbarum*, *Coniothyrium* spp., *Epicoccum nigrum*, *Phoma* spp., *Trichoderma viride* and various sterile mycelia. Only a few of the observed species were common to both litter and soil populations. According to Ruscoe (1971) the leaves of *Nothofagus truncata* in New Zealand were already substantially colonized by a variety of parasitic and saprophytic fungi when they reached the forest floor after leaf fall. These primary colonizers included *Phoma* sp., *Cladosporium herbarum*, *Alternaria tenuis*, *Epicoccum nigrum* and *Aureobasidium pullulans*. After leaf fall the leaves were invaded by new colonists, including species of *Penicillium*, *Stemphylium*, *Chaetomium* and *Trichoderma*.

Another forest type from the warm temperate zone of the southern hemisphere, namely a stand of *Eucalyptus regnans* F. Muell. in Victoria, Australia, has been studied by Macauley and Thrower (1966) who established a definite succession of fungi on the leaves during their decomposition. The initial litter fungi were species that had invaded the leaves on the tree, such as *Protostegia eucalypti*, *Readeriella mirabilis*, *Cytoplea* sp. and *Alternaria tenuis*, together with species which rapidly established themselves as saprophytes after the leaves had fallen, e.g. *Piggotia substellata* and *Hormiscium pinophilum*. A high proportion of these initial litter fungi were Coelomycetes, which were important internal colonizers of leaves in the early stages of decomposition. The frequency of the Coelomycetes tended to decrease with increasing decomposition, and in the final stage the mycoflora of the decomposed litter was similar to that of the A horizon of the soil

and included species of *Penicillium*, *Trichoderma*, *Mucor* and *Mortierella*. Some fungi occurred throughout the litter layer without any obvious distribution pattern, e.g. *Cladosporium herbarum*. Some species were predominantly litter surface colonizers (*C. herbarum*, *P. implicatum*, *M. ramanniana*), while others were internal colonizers (e.g. *Idriella* sp.). In some cases fungi, which first appeared in the succession as surface colonizers, entered the tissue in later stages of decomposition to become internal colonizers (e.g. *P. lapidosum* and *P. frequentans*).

The differences with regard to the mycoflora colonizing litter from different forest types may in part be due to occurrence of species-specific fungi, and in part to the use of different experimental methods. In spite of these differences, however, a general pattern of development of the litter mycoflora appears more or less clearly from the many investigations. At first the leaves are colonized on the tree by a variety of host specific or restricted parasites, accompanied by primary saprophytes, such as *Aureobasidium*, *Cladosporium* and *Epicoccum*, which seem to be common to many different tree species. After leaf fall there is intensive development of the fungi, including both the species already present and new colonizers from the litter layer, and during the later stages of decomposition the initial colonizers gradually disappear, being replaced by other forms. In the final stages, the mycoflora becomes more and more dominated by litter-decomposing Basidiomycetes and by typical soil fungi, mainly species of *Penicillium*, *Trichoderma*, *Mucor* and *Mortierella* (Hudson, 1968).

3. Yeasts in the Litter Layer

Yeasts do not constitute a very important part of the litter mycoflora, and little attention has been paid to this group of organisms. Saito (1956, 1966) mentions abundant occurrence of yeasts, mainly species of *Candida* and *Cryptococcus*, on old yellowish, mouldy leaves in the deeper layers of the litter of *Fagus crenata*. A new yeast species, *Candida corniculata*, was isolated from this material and described by Kuraishi (1958).

Hogg and Hudson (1966) found that the ballistospore-forming yeasts, which occurred abundantly in the phylloplane, still persisted 18 months after leaf fall as surface inhabitants of *Fagus sylvatica* litter. Two species, *S. roseus* and *T. minor*, were encountered in the samples in almost 100% frequency. In Denmark yeasts have been found to constitute from 1 to 4% of the colonies on dilution plates, inoculated with litter of *Fagus sylvatica*, corresponding to 85,000–360,000 yeast cells per g dry matter. Most of the strains isolated belonged to the genus *Torulopsis*, but *Sporobolomyces roseus*, *Hansenula saturnus* and species of *Cryptococcus*, *Candida* and *Rhodotorula* were also encountered.

In litter from a mixed *Quercus* wood in Belgium, Remacle (1970, 1971)

recorded numbers of yeast cells varying from 1·5 to 40 × 10^6 g^{-1} dry weight of leaves of *Quercus petraea*, and from 3 to 55 × 10^6 on leaves of *Carpinus betulus* L. The most common types were *Cryptococcus albidus*, *Torulopsis aeria* and various species of *Rhodotorula*.

B. The Litter Fauna

The abundance of Protozoa in the litter layer has been studied by Varga (1935), Volz (1951) and Schönborn (1962) in *Fagus* and *Quercus* stands in Germany, and by Stout (1962, 1963) in *Fagus* stands in England and *Nothofagus* stands in New Zealand. In general, both the number of individuals per g and the number of different species were found to be higher in the litter than in the soil beneath. Volz found 182,000 and 708,000 testaceans per m^2 of the two sites examined, and Schönborn found 3·8 × 10^6 m^{-2}. Stout found that the number of rhizopods varied from 1·2 to 21 × 10^6 m^{-2}, and that of ciliates from 0·8 to 5·4 × 10^6 m^{-2}, in both cases with the highest numbers in winter. According to Stout, the total protozoan fauna of the litter comprised about one hundred different species.

Forest litter also harbours large populations of nematodes (see Twinn, Chapter 13). Volz (1951) found numbers about 10^5 to 10^6 m^{-2} of the litter layer, and Stout (1962) found about 10^6 m^{-2} in summer and about 5 × 10^6 in winter. He also made estimates of the numbers of rotifers and copepods and found from 0·3 to 0·8 × 10^6 m^{-2} and from 0·2 to 1 × 10^6 m^{-2}, respectively, with the highest numbers in winter. van der Drift (1951) examined the populations of nematodes, tardigrades and rotifers in a Dutch *Fagus* stand. The results are not given in terms of numbers per unit area, but they probably correspond to several million nematodes and from 10^4 to 10^5 tardigrades and rotifers per m^2 of the litter layer. The nematodes were most numerous in the lower part of the litter close to the underlying soil, whereas the tardigrades and rotifers occurred in maximum numbers in the upper part of the litter. The number of nematodes in the litter layer of a Danish stand of *Fagus sylvatica* has been estimated recently to be *ca.* 150,000 m^{-2} (Yeates, 1972), and in the same stand the number of tardigrades in the litter layers was estimated to be 1500 m^{-2} (Hallas and Yeates, 1972).

The numerically dominant members of the mesofauna of forest litter and forest soils are the Acari (mites) and Collembola (springtails). According to Murphy (1953), Acari numerically constitute from 50 to 85% and Collembola from 14 to 40% of the total meso- and macrofauna in different forest soils. Similar results are presented by Maldague and Hilger (1963) for equatorial forests. Usually the number of Acari is 2–4 times the number of Collembola, and according to Nef (1957) the total populations of Acari and Collembola in the forest floor, including the underlying soil, in deciduous

stands can be estimated to about 400,000 m^{-2} and 200,000 m^{-2}, respectively. In addition to these two groups,the litter layer harbours a variety of other microarthropods and animals within the range of size of the mesofauna. Compared to the Acari and Collembola, however, these other animals are of little importance both numerically and with regard to influence on litter decomposition.

Among the macrofauna, the Lumbricidae are exceptional in that in a favourable environment they can influence the rate of litter decomposition more than any other group of soil or litter animals. Some species, such as *Dendrobaena octaedra* and *Lumbricus rubellus*, are confined mainly to the superficial organic horizons (L, F and H layers) and do not burrow in the mineral soil (Kühnelt,1961). More important, however, with regard to litter decomposition are the larger forms, e.g. *Lumbricus terrestris* and *Allolobophora longa*, which live in the mineral soil but get their food from the litter layer. The presence of these large earthworms is closely connected with the typical mull soil, largely because the mull condition is a result of their activity. If the environment is unsuitable for the large earthworms, a mor soil will usually develop, where only the small, litter-inhabiting earthworm species are present. According to Satchell (1967) the total biomass of earthworms in woodland mull soils can be estimated to be 100–250 g m^{-2}, whereas the biomass in mor soils probably in most cases does not exceed 2 g m^{-2} (Bornebusch, 1930; van der Drift, 1951).

In addition to the earthworms, large numbers of Enchytraeidae are found in the forest floor. On mor sites the biomass of Enchytraeidae may be equal to that of Lumbricidae, but on mull sites it is much smaller (Bornebusch, 1930). Among the other members of the macrofauna, only the large Diplopoda, such as *Glomeris* spp., and the larvae of Tipulidae, Bibionidae, Lycoriidae and Sciophilidae are of importance in the European deciduous forests (Zachariae, 1965). In the tropical zone the occurrence of Lumbricidae is usually sparse. Thus Madge (1965) in a tropical forest at Ibadan, Nigeria, detected only 34 specimens per m^2, weighing about 10 g, an amount comparable to that of mor soils in the temperate region. Instead tropical forests often harbour abundant populations of termites, which play an important part in litter decomposition. The populations have been estimated at 10^3–10^4 individuals per m^2 with a probable biomass of 5–50 g (Maldague, 1964, 1967; Lee and Wood, 1971).

C. The Roles of Animals and Micro-organisms in Litter Decomposition

1. Mechanical Disintegration of Litter

Often freshly fallen litter seems to be rather distasteful to the saprophagous litter fauna (see Lofty, Chapter 14, Edwards, Chapter 16), especially

the slowly decomposable types of litter, but the palatability is greatly improved by a period of weathering on the forest floor (van der Drift, 1951; Frömming, 1956; Ghilarov, 1963; Heath and King, 1964; Zachariae, 1965; Minderman and Daniëls, 1967). The most probable explanation is that substances distasteful to animals, e.g. polyphenols, are removed either by microbial breakdown or by leaching. The importance of polyphenols in the initial stages of decomposition has been demonstrated repeatedly (King and Heath, 1967; Satchell and Lowe, 1967; Feeney and Bostock, 1968).

For the slowly decomposable litter species the initial phase, therefore, will normally consist of an invasion of the dead tissue by micro-organisms, which under favourable conditions will occur soon after litter fall, when the litter has been thoroughly wetted on the ground. Under dry weather conditions the litter may remain more or less intact until it is covered by the next year's litter fall, whereby moisture conditions are improved. The more easily decomposable litter species with little or no polyphenolic or similar distasteful substances may be attacked almost immediately after leaf fall by the litter fauna, although growth of micro-organisms in this case will probably also improve the palatability.

It is generally accepted that the consumption of leaf material by the litter and soil fauna mainly results in a mechanical disintegration or comminution of the ingested material without much chemical change, and in most cases only a small proportion of the consumed food is digested and assimilated (Nef, 1957; Dunger, 1958*a*; Kuhnelt, 1961). Assimilation is in most cases confined to the easily decomposable carbohydrates and the soluble nitrogenous compounds in the leaf tissue, although bacteria and fungi ingested with the vegetable material may also contribute to the nutrition of the animals (Nielsen, 1962; van der Drift, 1965). The termites constitute an exception in this respect, as it has been demonstrated that they can digest and assimilate more than 50% of the consumed plant material (Lee and Wood, 1971). This efficiency, however, is due to a highly developed symbiosis with cellulolytic micro-organisms.

By the mechanical distintegration the exposed surface of the litter material is greatly increased and the access for micro-organisms to internal leaf tissues facilitated, and at the same time microbial activity is favoured by improved aeration and an increased water-holding capacity (van der Drift and Witkamp, 1960). Often pH increases during the passage through the intestinal tract, and the litter fragments may be intimately mixed with mineral or other materials, the main result being an acceleration of microbial activity.

The importance of the faunal activity can be observed in nature by comparing forest stands differing in this respect, and it has also been clearly demonstrated by direct experiments. One approach to this problem has

consisted in exclusion or reduction of the arthropod populations by addition of insecticides (e.g. naphthalene) to the decomposing litter (Kurcheva, 1960; Crossley and Witkamp, 1964; Witkamp and Crossley, 1966). Naphthalene effectively reduced the arthropod populations without suppressing the micro-organisms. On the contrary, Witkamp and Crossley found an increase in bacterial numbers after naphthalene application, so probably such experiments underestimate rather than overestimate the actual influence of the excluded arthropods. The greatest effect was observed by Kurcheva (1960), who also used the highest doses of naphthalene. The weight loss after 140 days was 55% for the untreated litter and only 9% for litter samples treated with naphthalene. In the experiments made by Witkamp and Crossley the untreated litter lost 60% of its initial weight in one year, compared to 45% for the naphthalene-treated litter.

Another approach has consisted in placing litter samples on the forest floor confined in bags of nylon net with different mesh sizes, thereby excluding different sections of the soil and litter fauna (Edwards and Heath, 1963; Heath *et al.*, 1964; Madge, 1965). Edwards and Heath found that *Quercus* and *Fagus* leaves disappeared three times as quickly from 7 mm mesh bags as from 0·5 mm mesh bags, and according to their observations fungi and bacteria contributed no visible effect to breakdown of leaves in the absence of soil animals. Heath (1961) found that leaf discs from which soil animals were excluded appeared to remain intact, and no significant decrease in weight per unit area occurred over a period of 12 months. Heath *et al.* (1964) similarly found that when *Quercus* and *Fagus* leaf discs were put into bags of very fine mesh (0·003 mm), which completely excluded soil animals, there was little breakdown in one season. Heath *et al.* (1966) compared the rate of disappearance of discs from a number of plant species, using bags of different mesh size. They found that the differences between the rates of disappearance from the large and small mesh bags, and consequently the importance of animal activity, were smaller for easily decomposable litter species than for litter that normally decomposes slowly, e.g. *Fagus* and *Quercus*. Madge (1965) made similar experiments in a tropical forest (Ibadan, Nigeria) and found that at the end of the experiments over 90% of the leaf discs remained untouched in the litter bags with the finest mesh (0·002 mm), whereas all leaf tissue in the bags with larger mesh sizes had been skeletonized.

Several attempts have been made to calculate the total amounts of litter material consumed annually by the animal populations. However, the estimates are all very uncertain, because of lack of knowledge of such fundamental things as the sizes of the populations and the feeding behaviour of the individual species. The difficulties of making such estimates are discussed in detail by van der Drift (1951). Dudich *et al.* (1952) and Nef (1957)

concluded that practically all litter materials pass through the intestinal tracts of the macro- and mesofauna during the initial phase of decomposition, and Dunger (1958*b*, 1960) stated that at least on mull sites the total saprophagous fauna is able to consume all (or almost all) the dead plant material added annually to the forest floor. On mor sites the litter material may retain its original structure for several years, unaffected by animal consumption.

According to Satchell (1967) the potential consumption of the large populations of earthworms in fertile mull soils may substantially surpass the annual litter fall. In tropical forests, where earthworms are scarce, termites may play a similar role. It has been estimated that termite populations can consume up to 7 t ha^{-1} of organic material annually (Maldague, 1964, 1967), and the rapid disappearance of the fallen litter in tropical forests is often due largely to the activity of ants and termites (Lee and Wood, 1971).

2. Chemical Changes during Litter Decomposition

The chemical breakdown of dead plant material is generally believed to be a result mainly of fungal and bacterial metabolism. Although the fauna under favourable conditions may consume the entire litter fall, only 5–10% of the material is metabolized by the primary consumer. The defaecated material may be eaten again by other animals, but the total metabolism will probably seldom exceed 20%, leaving 80% or more to be decomposed by the microflora. Macfadyen (1963) estimated the total annual metabolism of the soil and litter fauna on a mull site to be 491 kcal m^{-2}, which is the calorific content of *ca.* 100 g litter, corresponding probably to about 20% of the available material.

The chemical changes occurring during the initial stage of litter breakdown consist in decomposition of soluble carbohydrates, starches, pectins, and soluble nitrogenous compounds, and the micro-organisms responsible for this initial attack comprise a variety of bacteria and fast-growing fungi. The decomposition usually occurs so rapidly that it is difficult to detect appreciable quantities of these substances in natural litter (Burges, 1967). Other soluble substances, such as polyphenols, also tend to disappear during the initial phase of litter decomposition.

A considerable proportion of the inorganic ions in the fallen leaves is rapidly lost by leaching. Remezov (1961) found that 80–90% of the initial amount of potassium was lost in one year and often already during the early spring period. According to Burges (1967) much of the sodium and potassium is washed out within a few weeks. Phosphate and magnesium were also fairly rapidly mobilized, but about half of the calcium remained in the plant material. Attiwill (1968) found that the loss of elements from

decomposing litter of *Eucalyptus obliqua* L'Herit, followed the order Na > K > Ca > Mg > P. About 90% of the sodium and potassium disappeared during the first year, whereas about half of the other three elements still remained in the litter after two years.

The decomposition of cellulose often occurs mainly during the second wave of microbial activity following the mechanical disintegration of the litter material. Some cellulose is broken down already during the passage of plant material through the soil and litter animals, some of which have special fermentation chambers in their intestinal tract harbouring cellulolytic bacteria (Koch, 1967). Populations of cellulolytic bacteria may also be present in the intestines of earthworms and enchytraeids (Nielsen, 1962), but most of the cellulose is broken down by non-symbiotic microorganisms, and fungi probably play the most important part in cellulose decomposition in forests.

The most resistant of the compounds occurring in appreciable quantities in litter material is lignin. The percentage of lignin therefore tends to increase during the initial stages of litter decomposition. Occurrence of ligninolytic bacteria has been reported (Sørensen, 1962), but it is generally assumed that decomposition of lignin under natural conditions is carried out exclusively by soil Basidiomycetes (Lindeberg, 1947; Mikola, 1958; Garrett, 1963; Hering, 1967). These are rather slow-growing organisms, and they do not develop in the loose litter layer. Their activity mainly takes place in the final stage of litter decomposition in the F or H horizons or after incorporation of the material into the mineral soil. The initiation of the Basidiomycete phase is apparently associated with the increased density and much higher moisture content of the litter material at this stage (Burges, 1965).

D. Decomposition Rates

When discussing decomposition rates, it is important to distinguish between rate of disappearance of the fallen litter from the soil surface and the rate of complete chemical breakdown (mineralization) of the organic litter components. In the former case, only the first part of the decomposition, viz. disintegration and incorporation into the organic fraction of the soil, is considered, whereas in the latter case the mineralization of the organic matter is also taken into consideration. Normally the rate of mineralization will be correlated with the rate of disappearance, but the correlation need not be very close. In the classic paper by Romell (1932) it is emphasized that even if the litter disappears much more rapidly on mull than on mor sites, the rate of mineralization may be almost the same.

In deciduous forests the rate of disappearance of litter can be estimated

simply by determining the weight per unit area of the litter layer before and after the annual litter fall (Remezov, 1961; Witkamp and van der Drift, 1961; van der Drift, 1963, 1965; Zavitkovski and Newton, 1971). By this method the disappearance rate is determined under completely natural conditions, but difficulties may arise because of the often very uneven distribution of the litter on the ground.

Another widely used method consists of placing weighed samples of litter on the forest floor, confined by layers of glass wool (Mikola, 1954, 1960), in bags of nylon net (Bocock and Gilbert, 1957; Bocock *et al.*, 1960; Gilbert and Bocock, 1960; Bocock, 1964; Shanks and Olson, 1961; Witkamp, 1963; Witkamp and Crossley, 1966; Maldague, 1967), in terylene bags (Madge, 1965), in fibreglass net bags (Witkamp, 1966) or in wire boxes (Attiwill, 1968). In some cases, leaf discs have been used instead of whole leaves (Heath *et al.*, 1964, 1966). In the confined litter samples conditions are approximately natural, but the leaves in the bags tend to be more closely packed and more humid than in the undisturbed litter layer. Furthermore, the possibilities for larger animals to move whole leaves or large leaf fragments are limited by the mesh size. In order to avoid these sources of error, individually tethered leaves have been used instead of the litter bags. Witkamp and Olson (1963) found that *Quercus* leaves decayed more than twice as fast when tethered and otherwise free, than when confined in litter bags, whereas Woodwell and Marples (1968) found only a slight increase in the rate of decay measured by the tethering technique as opposed to enclosing the litter in bags.

The rate of disappearance can also be calculated, if the total annual litter fall and the total amount of litter material accumulated on the forest floor are known, on condition that a state of equilibrium has been reached. Simple formulas for the calculation of a loss constant or decomposition coefficient were stated by Jenny *et al.* (1949) and further elaborated by Olson (1963). Such calculations have been carried out for many different forest types (Laudelot and Meyer, 1954; Nye, 1961; Kira and Shidei, 1967; Jung, 1969; Andersson, 1970: Reiners and Reiners, 1970; Nihlgård, 1972), and the method can be used to determine not only rates of disappearance of litter from the soil surface, but also rates of mineralization of the organic material. Furthermore, turnover times of various fractions of the litter material can be calculated (Reiners and Reiners, 1970).

The decomposition rate is affected, among other things, by differences in decomposability between leaf litter of different tree species, and many different properties of litter have been put forward as possible reasons. In laboratory experiments, where faunal activity was excluded, Broadfoot and Pierre (1939) and Lossaint (1953) found that the most important factors controlling the decomposition rate were the contents of water-soluble

organic matter, nitrogen, excess-base and calcium. The soluble organic substances were important mainly in the initial phase, and excess-base and soluble calcium during the later stages of decomposition. The rate of disappearance of different litter species due to animal activity, especially that of earthworms, has also been studied in laboratory experiments (Lindquist, 1941; Bornebusch, 1946; Satchell and Lowe, 1967), and again litter rich insoluble organic matter and nitrogen disappeared most rapidly. However, Satchell and Lowe also found a strong correlation between the palatability of the litter and its content of taste substances, especially polyphenols, whereas the mechanical nature of the litter seemed to be of small significance, at least in relation to the large earthworms.

Comparison of different litter species has also been carried out extensively by field experiments, either using the litter-bag method (Bocock and Gilbert, 1957; Bocock *et al.*, 1960; Gilbert and Bocock, 1960; Bocock, 1964; Shanks and Olson, 1961; Heath and King, 1964; Heath *et al.*, 1966; Witkamp, 1963, 1966) or by placing litter samples directly on the soil surface (Wittich, 1939, 1943, 1953; Sjörs, 1959; Froment and Mommaerts-Billiet, 1969; Mommaerts-Billiet and Froment, 1969). The results of the field experiments on the whole agree with those of the laboratory experiments. Litters rich in nitrogen and soluble carbohydrates and poor in polyphenols, such as those of *Fraxinus* spp., *Alnus* spp., *Sambucus nigra* L., *Corylus avellana* L. and *Ulmus* spp., decompose rapidly, whereas litters of *Quercus* spp. and especially *Fagus* spp. are relatively resistant.

Wittich especially emphasized the C:N ratio as an important factor, and he found by comparison of litters from the same tree species, but with varying calcium content, that this did not affect the decomposition rate. He also found that the lignin content was of small significance. Easily decomposed litter may have a high lignin content (Wittich, 1939). Bocock (1963) found that addition of nitrogen-rich material (caterpillar frass) to decomposing *Quercus* litter did not accelerate the decomposition, so that in this case factors other than available nitrogen must have been limiting. According to Olson and Crossley (1963) and Witkamp (1966) the differences in decomposability between different litter species are most prominent during the initial stages of decomposition, and the species influence decreases with progressing decay and increasing contact with soil and soil animals.

The decisive influence of climate on disappearance of litter can be clearly demonstrated by comparing the calculated decomposition coefficients or by direct observation of the progress of litter decay in different climatic zones. In a tropical rainforest the fallen leaves may lose their structure in two weeks (Bates, 1960), whereas in the cool temperate zone the same process takes months or even years. In the tropical zone, moisture is often a limiting

factor (Madge, 1965; Hopkins, 1966), while in the temperate zones moisture or temperature may be the decisive factor, depending on local conditions (Edwards and Heath, 1963; van der Drift, 1963). Mikola (1960) compared the decomposition rates of forest litter in different parts of Finland and found about 40% higher weight loss from litter in southern Finland than from litter in similar conditions in northern Finland, and he concluded that the decisive factor was the temperature during the growing-season, whereas moisture conditions hardly played any role.

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